
The origin and early evolution of whales: macroevolution documented on the Indian Subcontinent

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The origin of whales (order Cetacea) from a four-footed land animal is one of the best understood examples of macroevolutionary change. This evolutionary transition has been substantially elucidated by fossil finds from the Indian subcontinent in the past decade and a half. Here, we review the first steps of whale evolution, i.e. the transition from a land mammal to obligate marine predators, documented by the Eocene cetacean families of the Indian subcontinent: Pakicetidae, Ambulocetidae, Remingtonocetidae, Protocetidae, and Basilosauridae, as well as their artiodactyl sister group, the Raoellidae. We also discuss the influence that the excellent fossil record has on the study of the evolution of organ systems, in particular the locomotor and hearing systems.

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1. Introduction

In 1936, Remington Kellogg, the authority on fossil whales of his day, observed that no fossil whales had been found in the Indian Subcontinent, and that there was ‘very strong evidence that they had not as yet invaded these regions.’ Kellogg’s inference, though reasonable at the time, has been proven wrong by a string of important fossil discoveries in India and Pakistan, starting with the discovery of fossil whales in Kutch, Gujarat (Sahni and Mishra 1972, 1975), and continuing most recently with the recognition that *Indohyus*, a small deer-like animal from the Himalayas, is a close relative of whales (Thewissen *et al.* 2007) and with several complete fossil whale skeletons from the Sulaiman Range in Pakistan (Gingerich *et al.* 2009).

The discoveries of the last twenty years in the Indian Subcontinent have transformed our understanding of whale evolution. Whereas twenty years ago, the origin of whales was documented solely by very fragmentary fossils, at present, the origin of whales may very well be the best

understood example of macroevolution in the fossil record (Thewissen *et al.* 2009).

This article discusses the first thirteen million years of whale evolution, the period in to which the Indian subcontinent has contributed most significantly. These thirteen million years cover the transition from land to water, the origin of whales (at around 50 million years ago), and the first fully aquatic cetaceans (at around 37 million years ago). These early cetaceans lived in the Eocene Epoch (55 to 37 million years ago) and are collectively referred to as archaeocetes. Cetacean evolution continued with the origin of the two modern suborders, the odontocetes (toothed whales, which includes dolphins and porpoises) and the mysticetes (baleen whales). Good summaries of their evolution can be found in Fordyce and de Muizon (2001), and Biannuci and Landini (2007).

Here, we review the first steps of whale evolution: the transition from four-footed land animals to obligate marine predators. We discuss the groups of early whales that document the transition from land to water, emphasizing what is known about their morphology (from studying fossils)

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and habitats (from studying the rocks in which fossils are found). We also explain how fossils have contributed to our understanding of the phylogenetic relations of whales to other mammals, and the role that DNA sequencing studies of the whale genome have played. Then, in order to illustrate how complete the fossil record is, we will discuss the evolution of two organ systems: locomotion and hearing. Using these two organ systems, we explain the intricate interaction between morphology and function, how evidence from studies of modern animals can be used to understand fossil morphologies, and how understanding of fossil morphologies leads to insights regarding modern functional morphology and enriches understanding of developmental biological patterns.

2. Whales are mammals

Cetacea are an order of placental mammals. Cetacea includes whales, dolphins and porpoises, but palaeontologists commonly use the term whales as a synonym for all of Cetacea. All modern Cetacea are obligate aquatic mammals: they die when they are on land. Modern, but not all fossil, cetaceans have streamlined bodies, with fins (called flippers) for forelimbs, a horizontal tailfin (called the fluke) at the end of the tail, and there are no external hind limbs, although external hind limbs are present in their embryos (Thewissen *et al.* 2006; figure 1).

It has been known for a long time that cetaceans were mammals because they have two characters known only in mammals: cetaceans nurse their young with milk and some have (sparse) hairs on their bodies. Because mammals originated on land, this implies that cetaceans had land ancestors, and that, in evolution, the ancestors of cetaceans underwent a transition from living on land to living in water.

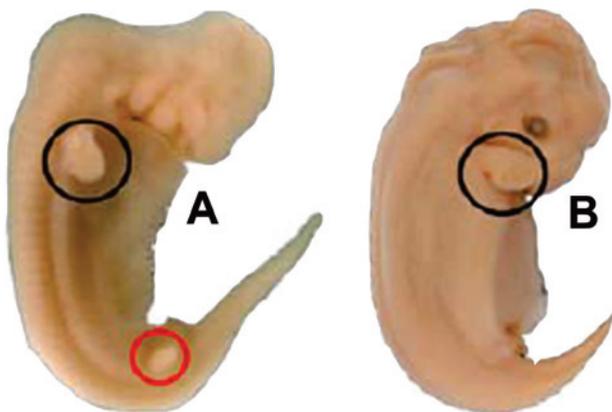


Figure 1. Embryos of pantropical spotted dolphin, *Stenella attenuata*, around 4 to 9 weeks of gestation. Note the presence of forelimb (black circle) and hindlimb (red circle) buds in the first embryo (A). All external traces of hind limb disappear later in development (second embryo) (B).

This implication was already clear to Charles Darwin (1859) when he speculated in *The Origin of Species* that these early transitional forms may have looked like swimming bears catching insects with their open mouth. However, actual fossils of cetaceans that are transitional between land and water have only been found in the past twenty years.

3. Diversity of early whales

Given that modern cetaceans hunt live prey and that some fossil cetaceans had teeth resembling those of carnivores, it was generally believed that cetaceans were related to insectivore or creodont (archaic carnivorous) mammals (Kellogg 1936). This changed in 1966, when Van Valen compared early cetaceans to fossil ungulates, and found that cetacean dental morphology was close to the extinct mesonychid ungulates, and that the two groups were closely related. Mesonychid affinities to cetaceans were generally accepted by palaeontologists since then, but did not coincide with the results of molecular studies in the last decades of the twentieth century. Molecular evidence steadily accumulated, first from protein studies, later from nuclear and mitochondrial DNA (reviewed by Gatesy and O'Leary 2001), and from SINEs (Nikaido *et al.* 1999) that cetaceans were closely related to artiodactyls (even-toed ungulates, such as the pigs, hippopotamus, camels, deer, giraffes, cattle, and goats). Within this group, most molecular data suggest that cetaceans are the sister group to hippopotamids (e.g. Shedlock *et al.* 2000; Price *et al.* 2005). Molecular systematists have proposed the name Cetartiodactyla for the order of mammals that includes artiodactyls and cetaceans, as a replacement for the order names Artiodactyla and Cetacea, although this name is not widely accepted.

Palaeontological studies only fell in line with the molecular point of view in 2001, when ankle bones of two Eocene cetaceans from Pakistan were discovered (Gingerich *et al.* 2001; Thewissen *et al.* 2001). The astragalus (also called the talus) is the ankle bone on which the foot hinges on the tibia (shin bone). The articular surface has the shape of a trochlea (or pulley) on the proximal side of the astragalus. A second joint occurs on the distal side (called head) of the astragalus, and this joint is usually a ball joint. The head of the astragalus of artiodactyls is unique among mammals in having the shape of trochlea (Schaeffer 1947; figure 2). In 2001, it was discovered that in early whales the head of the astragalus was trochleated (Gingerich *et al.* 2001; Thewissen *et al.* 2001), and phylogenetic analyses taking this into account convinced most palaeontologists that the molecular phylogenies were correct and that cetaceans were close relatives of artiodactyls (Thewissen *et al.* 2001; Geisler and Uhen 2003; Geisler *et al.* 2007).

This finding led palaeontologists to search for the closest relative of cetaceans among the artiodactyls. Although

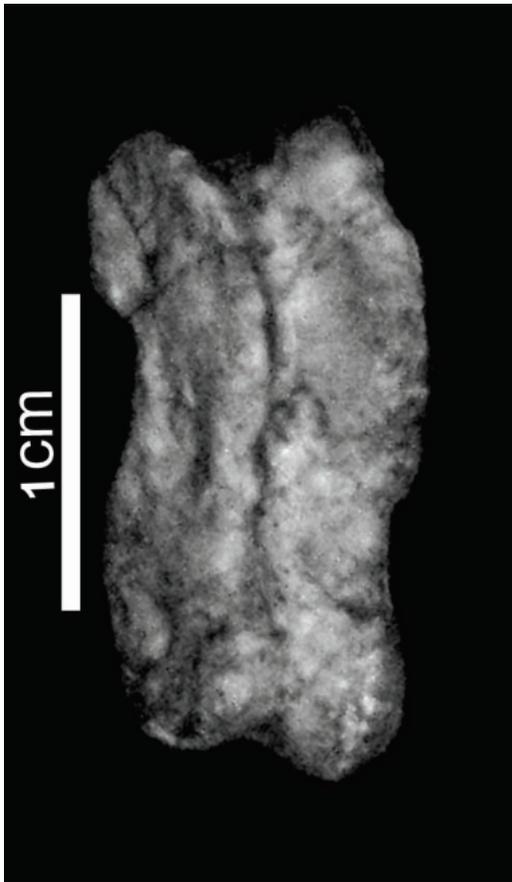


Figure 2. Astragalus (talus) of *Indohyus* (RR 246; see Thewissen *et al.* 2007) from Sindhkatuti, Jammu and Kashmir, India.

the molecular evidence indicated that the closest modern relative of cetaceans was hippopotamids, the fossil record of this family only goes back to 15 million years (Boisserie *et al.* 2005), whereas the oldest whales are more than 50 million years old. Fragmentary fossils of the Indian endemic artiodactyl family Raoellidae suggested that these might be closely related to cetaceans (Geisler and Uhen 2005), and more complete fossil material for raoellids from Jammu and Kashmir exposed this link clearly (Thewissen *et al.* 2007). Current phylogenetic work indicates that raoellids are the closest sister clade to cetaceans, and that hippopotamids are the sister group to the combined raoellid-cetacean clade (Geisler and Theodor 2009).

The raoellid in question, *Indohyus*, was originally described by Ranga Rao (1971) on the basis of dental material. It was somewhat larger than cat, and had delicate slender limbs. Although the skull of *Indohyus* (figure 3) was that of an even-toed ungulate, its middle ear showed some unusual similarities with that of early whales, and cladistic analyses suggested that *Indohyus* was the closest relative to whales (figure 4; Thewissen *et al.* 2007). *Indohyus*

was found in sediments that are approximately 47 million year old, although the family Raoellidae was probably in existence long before that. A large number of bones, mixing the skeletons of many individuals were found in river deposits, and two factors indicate that *Indohyus* spent part of its life in the water. The first is that the cortical layer of the limb bones of *Indohyus* is very thick (a phenomenon called osteosclerosis) as is common in wading mammals as an adaptation to counteract buoyancy. The second indication comes from the biogeochemistry of its teeth, which suggest that *Indohyus* lived in water (Thewissen *et al.* 2007).

The most archaic whales are pakicetids, a family only known from a few localities in northwestern India and northern Pakistan. Pakicetids did not look like whales, they had long slender limbs, and a long narrow tail (Thewissen *et al.* 2001; Madar 2007). The sediments in which pakicetids are found indicate that the climate was hot and dry, and these whales are only found in shallow, ephemeral freshwater streams. The largest pakicetids were similar in size to a wolf, and it is not likely that these waters were sufficiently deep for pakicetids to swim. Just like *Indohyus*, pakicetids also had osteosclerotic limb bones suggesting that these whales were waders, not swimmers (Grey *et al.* 2007). Pakicetid fossils are approximately 50 million years old, although it is likely that the family had a longer temporal range. There are three genera of pakicetids, *Ichthyolestes*, *Pakicetus*, and *Nalacetus*. The first of these to be described was *Ichthyolestes* (Dehm and Oettingen-Spielberg 1958) but the material was very fragmentary and the authors did not recognize it as a cetacean. West (1980) was the first to recognize pakicetid fossils as cetaceans. Complete skeletal material for pakicetids was described by Thewissen *et al.* (2001), Nummela *et al.* (2006) and Madar (2007).

Ambulocetids represent the next diverging family of archaic cetaceans, and these are also only known from a few sites in Pakistan and India. These whales were large and crocodile-like, and lived amphibiously (Thewissen *et al.* 1994, 1996; Madar *et al.* 2002). The sediments in which ambulocetids are found indicate that these whales lived in a coastal environment. Ambulocetids had large feet and a strong tail, but were also osteosclerotic (Grey *et al.* 2007) indicating that they were not fast pursuit predators like modern cetaceans. It is likely that ambulocetids were ambush predators. The genera of ambulocetids are *Ambulocetus*, *Gandakasia*, and possibly *Himalayacetus*. *Himalayacetus*, from the Simla Hills of Himachal Pradesh is commonly considered the oldest known whale, as the rocks in which it was found contain microfossils that are 53.5 million years old (Bajpai and Gingerich 1998). *Ambulocetus* and *Gandakasia* were found in rocks approximately 49 million year old.

Another family of amphibious cetaceans is Remingtonocetidae. This family, initially characterized by Kumar and Sahni (1986), is also only known from India and

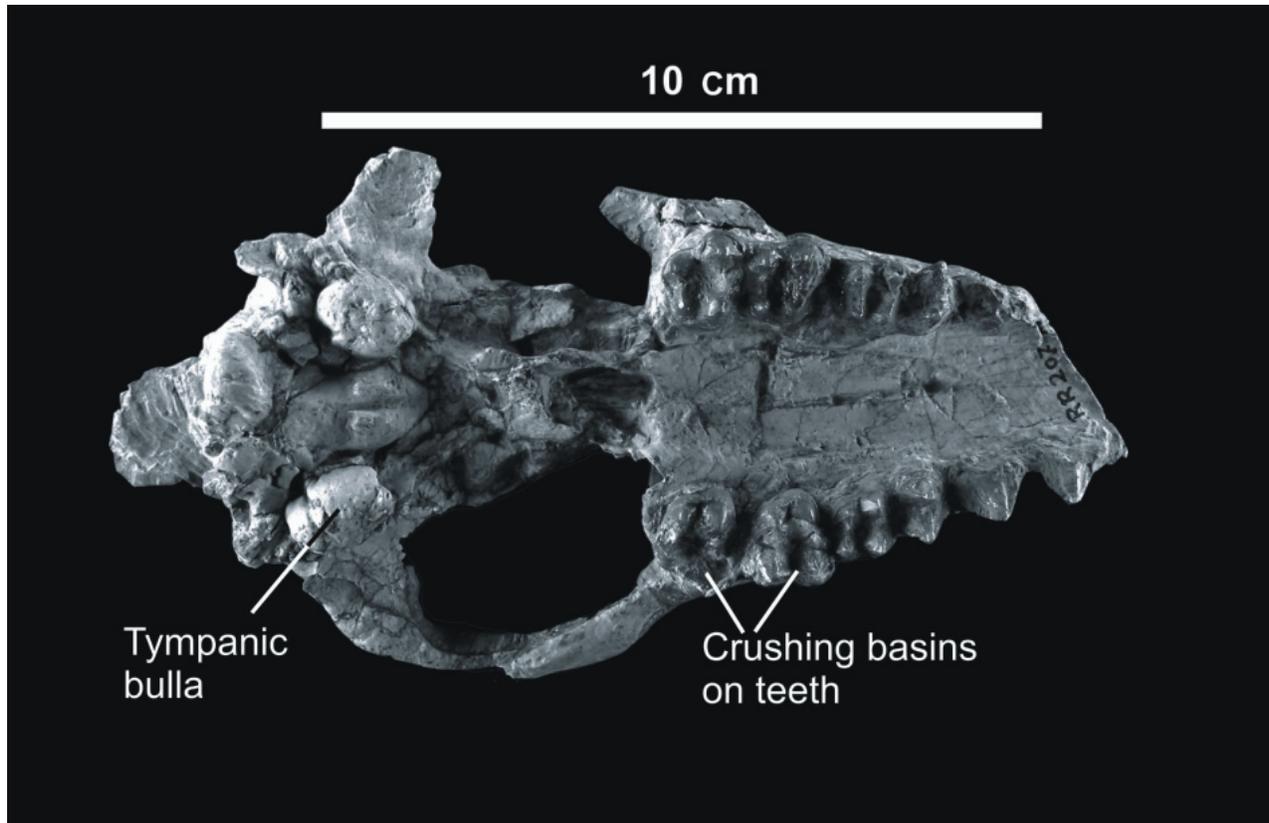


Figure 3. Skull of *Indohyus* (RR 207; see Thewissen *et al.* 2007) from Sindhkatuti, J&K. This small artiodactyl is the closest known relative of ancestral whales.

Pakistan. The remingtonocetid for which the best skeleton is known is *Kutchicetus* from Kutch, Gujarat (Bajpai and Thewissen 2000; Thewissen and Bajpai 2009). *Kutchicetus* had short limbs, but a strong, powerful tail with vertebrae that were flattened. It was able to live on land, but probably swam with its tail. All remingtonocetids are characterized by a long, narrow snout and small eyes (figure 5, Thewissen and Bajpai 2009). The size of the eyes and the morphology of the ear probably indicate that their vision was poor, and that hearing was the dominant sense (Nummela *et al.* 2007; Thewissen and Nummela 2007). Sedimentological evidence indicates that remingtonocetids lived in protected coastal areas of Kutch, such as bays and swamps, where the water may have been turbid (Bajpai and Thewissen 1998; Thewissen and Bajpai 2009). The genera of remingtonocetids are *Andrewsiphius*, *Attockicetus*, *Dalanistes*, *Kutchicetus*, and *Remingtonocetus*.

Protocetids are the next family in the phylogenetic tree of cetaceans. In addition to the Indian continent, protocetids are known from Africa, North America, and they were recently discovered in South America (Uhen 2008). The ability of protocetids to colonize the oceans of the world implies that they were strong swimmers. Their skeletons show the presence of strong hind limbs and a powerful tail. In spite

of a great diversity of protocetids, relatively complete skeletons are known for a few taxa only: *Rodhocetus*, *Artiocetus*, *Maiacetus* from the Indian subcontinent (Gingerich *et al.* 1994, 2001, 2009) and *Georgiacetus* from North America (Hulbert 1998; Hulbert *et al.* 1998). Skulls and lower jaws are known for many more taxa (figures 6, 7), and the robustness of the teeth, and the structure of the jaws indicates that there was great diversity in masticatory function. As a result, it is likely that diet and feeding habits varied among members of this family.

Protocetids are often found in sediments that indicate carbonate platforms (Williams 1998), places in shallow oceans where calcium carbonate is deposited, such as reefs. The formation of carbonate platforms implies shallow, clear, and relatively warm water. In the period that protocetids lived, from 47 to 41 million years ago, the Mediterranean Sea was wider, and the Arabian Peninsula and Central America were largely submerged. As a result, there was a continuous tropical ocean around the globe that allowed protocetids to disperse to many continents, and greatly affected cetacean evolution (Fordyce 2008).

After protocetids, basilosaurid cetaceans came to dominate the oceans (Kellogg 1936). These cetaceans were

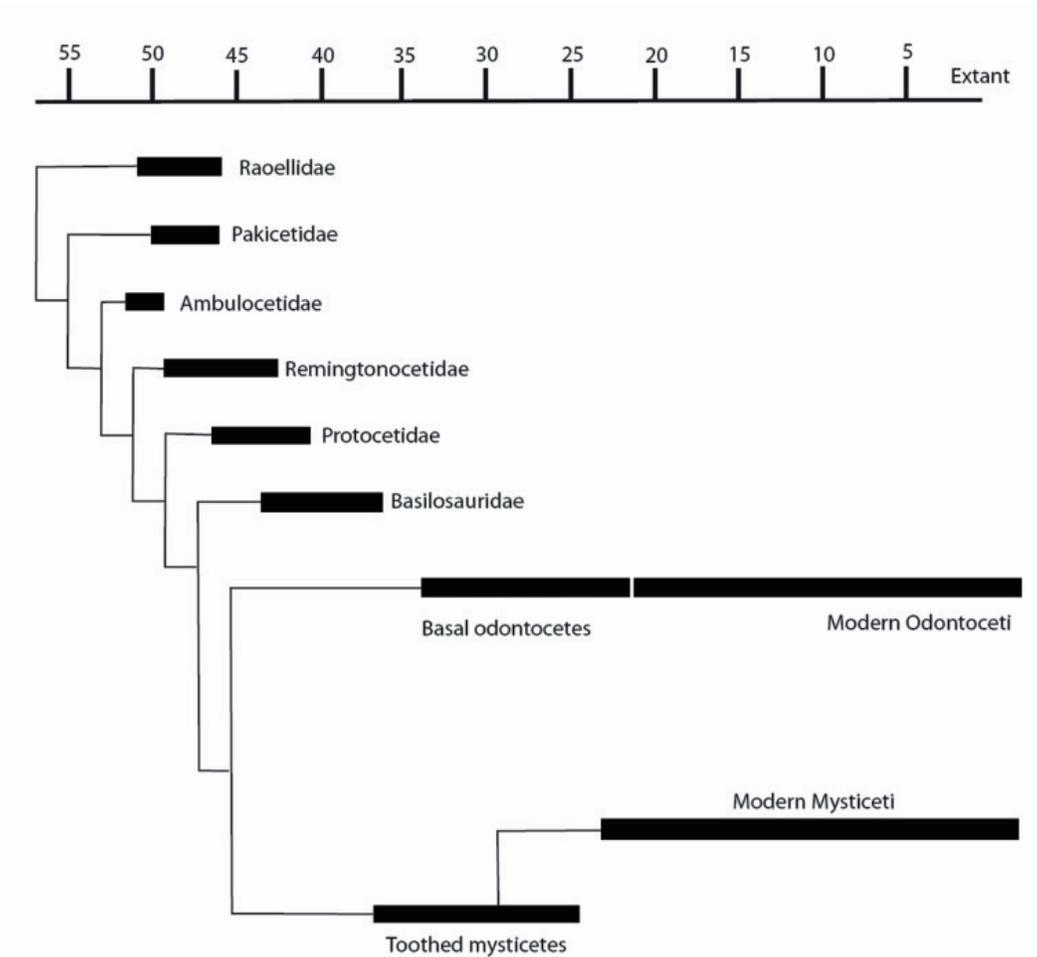


Figure 4. Ranges (in million years) and phylogeny of Eocene and modern cetaceans and raoellid artiodactyls.

obligately aquatic, having tiny hind limbs and flipper-shaped forelimbs (Gingerich *et al.* 1990; Uhen 2004). In spite of having bodies that looked like modern cetaceans, basilosaurids had heads that lacked the specializations of modern odontocetes and mysticetes: they did not echolocate and lacked baleen. Some of these whales reached large sizes; the genus *Basilosaurus*, known from Africa and North America, had a snake-like body 17 m long. Smaller basilosaurids, such as *Dorudon*, probably lived more like modern dolphins.

Around 37 million years ago, archaeocetes went extinct and the two modern suborders, Odontoceti and Mysticeti originated (Fordyce and Muizon 2001; Fordyce 2008).

4. Locomotion

All modern whales swim by moving their tail fluke through the water in a vertical plane, although the flukes are assisted, especially when turning, by the flippers. Just like modern cetaceans, *Indohyus* and pakicetid cetaceans lived in water.

However, these were slow waders or bottom walkers, similar to modern *Hippopotamus*. It is unlikely that these mammals were fast swimmers because the limb bones with their thick cortical layer would significantly increase inertia and drag. In contrast, most modern whales have very thin cortical bone (Madar 1998; Grey *et al.* 2007) and are built lightly, able to swim fast underwater.

Our understanding of locomotor evolution in whales is inspired by studies of modern mammalian swimming. Modern swimming mammals, such as minks, polar bears, seals, sealions, otters, and otter shrews, swim in a great variety of ways. Some mostly propel themselves with all four limbs (ferrets, Fish and Baudinette 2008) or their forelimbs (forelimb paddling in polar bears) or their hind limbs (hind limb paddling in the waterpossum *Chironectes*). Others undulate their entire body (caudal undulation in river otters; Fish 1994), or move their foreflippers through the water in movements that resemble that of a bird wing in flight (pectoral undulation in otariid sealions). The locomotor efficiency of these different means of swimming was studied by Frank

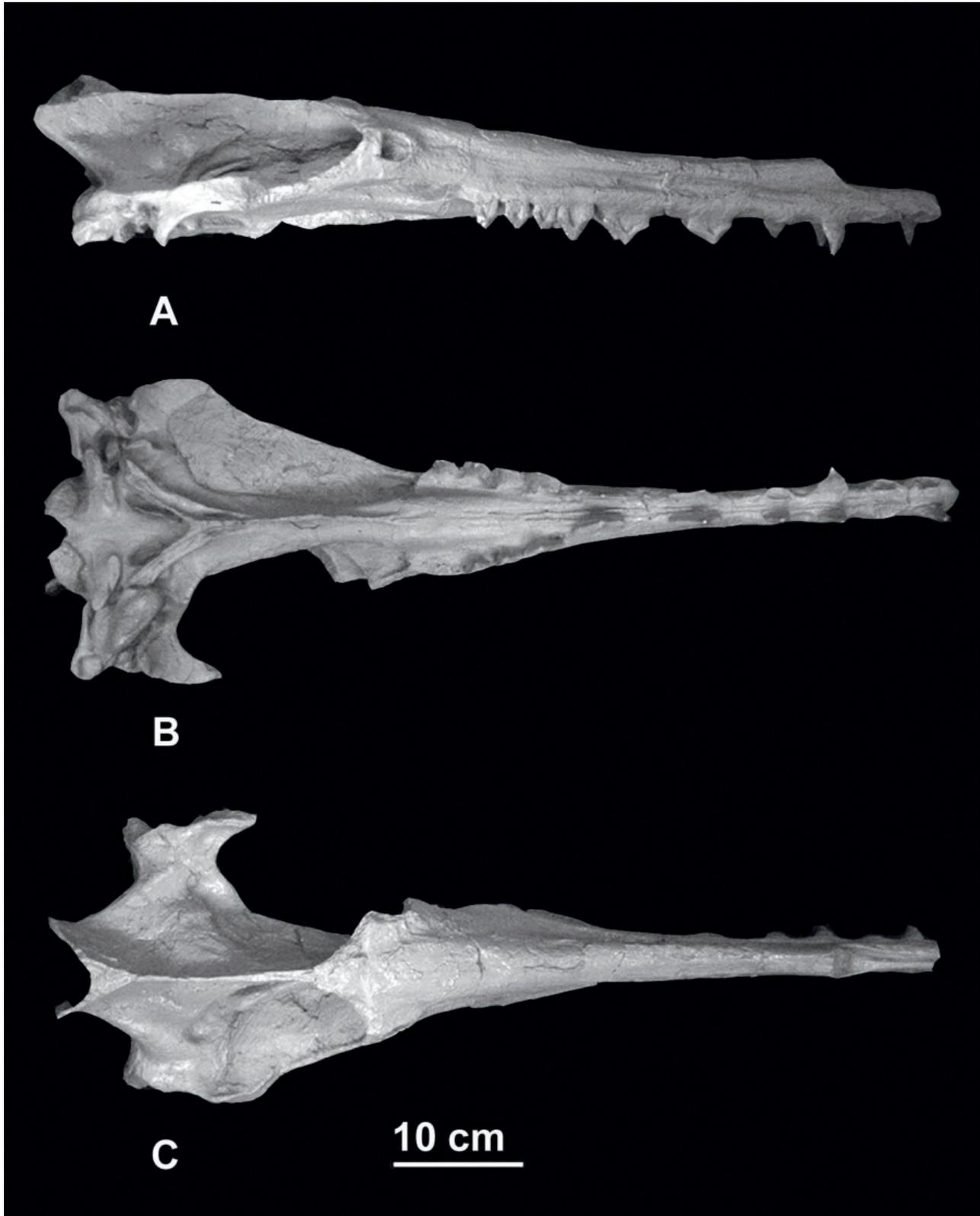


Figure 5. Skull of *Remingtonocetus* (IITR-SB 2770) from Kutch, Gujarat, in lateral (A), ventral (B) and dorsal (C) view. Note the small size of the orbits (implying the presence of small eyes), and the long, narrow snout.



Figure 6. Mandible of the protocetid cetacean *Babiacetus mishrai* from Kutch, India (Holotype, IITR-SB 2512; Bajpai and Thewissen 1998). The jaw of this protocetid is very narrow, and shows a fused mandibular symphysis.

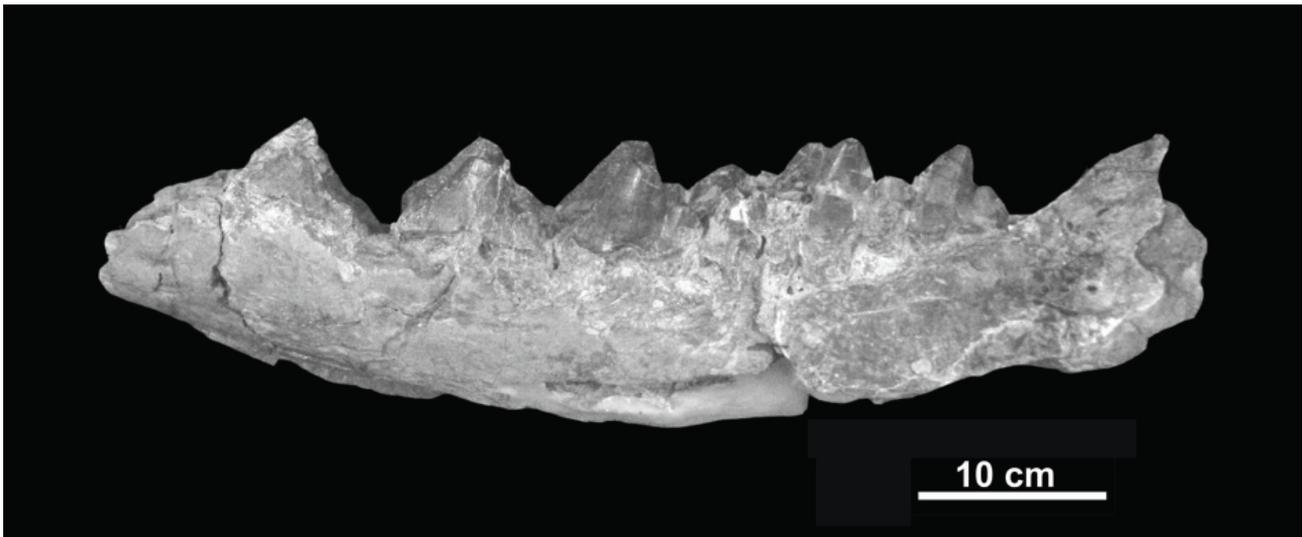


Figure 7. Mandible of *Gavaiacetus sahnii* (IITR-SB 3189), a protocetid cetacean from Kutch. Note the large size and stout teeth of this species.

Fish, who also proposed (Fish 1996, 2000) an evolutionary model for mammalian swimming modes based on studies of energetic and kinematics of mammals in flowtanks. Based on this model, Thewissen and Fish (1997) proposed a model for the evolution of swimming in cetaceans, and found that many of the inferred locomotor stages of cetaceans occur in modern otters (lutrine carnivores; Fish 1994).

The earliest cetaceans, although not dedicated swimmers, probably paddled with their hind limbs when

swimming (Thewissen *et al.* 2001), movements powered by limb muscles or by muscles along the vertebral column (Madar 2007). Thewissen and Fish (1997) found that *Ambulocetus* had body proportions similar to those of modern pelvic paddlers in which the feet are much larger than the hands. Motions of the hind limbs in the dorsoventral plane can be powered by undulations of the vertebral column, consistent with work by Buchholtz (1998) who proposed that *Ambulocetus* and *Remingtonocetus* undulated

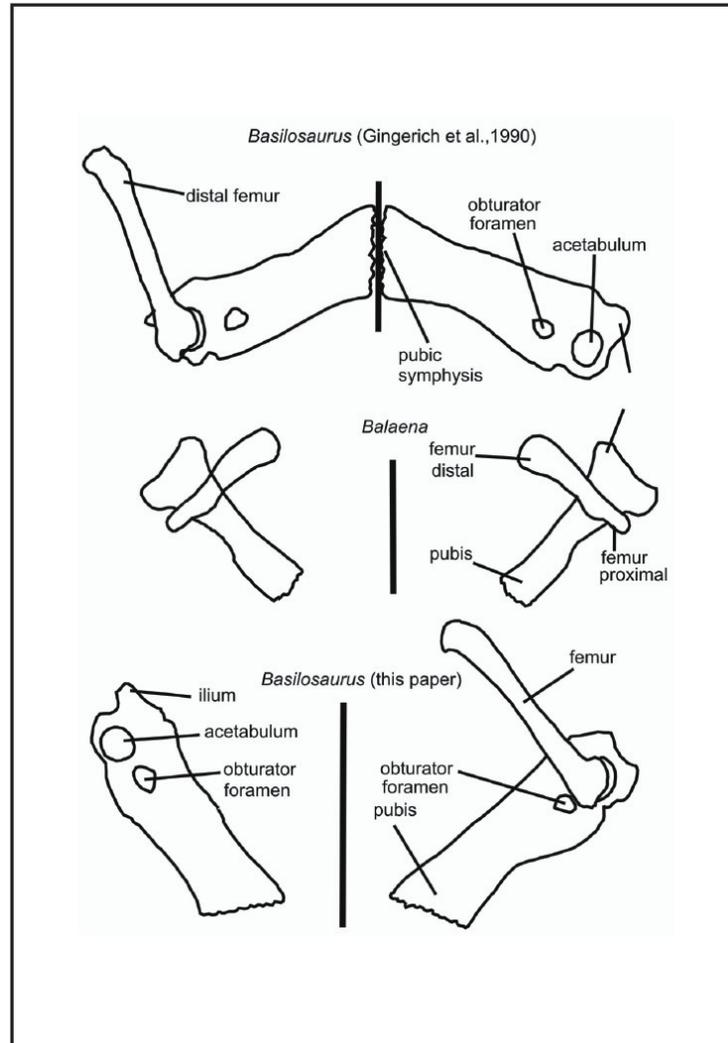


Figure 8. Ventral view of left and right innominate and femur of *Basilosaurus* (as interpreted by Gingerich *et al.* 1990, but reconstructed in a different view), modern *Balaena mysticetus* (see Thewissen *et al.* 2009) and new interpretation of position of innominate in *Basilosaurus*. Note that in top image, the ilium is directed laterocaudal, and the obturator foramen is mediocranial to the acetabulum, whereas bottom image is more consistent with position in *Balaena* as well as modern land mammals. Position of femur in *Basilosaurus* is variable as this bone was probably movable in the animal. Heavy line indicates the ventral midline.

their vertebral columns and used these movements to power their feet.

The tail was long and powerful in the remingtonocetid *Kutchicetus*, and Bajpai and Thewissen (2000) proposed that the tail provided most of the propulsive force, as in the modern otter *Pteronura*. This mode of locomotion, caudal undulation, is also predicted by the locomotor model of Thewissen and Fish (1997), as explained by Thewissen and Williams (2001). The innominate of *Kutchicetus* is similar to that of other early cetaceans, in particular pakicetids (Madar 2007) and *Ambulocetus* (Thewissen *et al.* 1996). All three taxa are characterized by large ischial tuberosities, the area where the adductor muscles of the thigh would attach. The femur in these animals is short, and matches

the (estimated) distance between acetabulum and ischial tuberosity. Therefore, adductor muscles extending between ischial tuberosity and proximal tibia would have run mostly mediolaterally, and functioned most efficiently as adductors (unlike many mammalian quadrupeds, where they are important dorsiflexors of the hip).

Taken together this evidence suggests that the different types of aquatic locomotion occurring in modern mustelids (*Mustela vison*, *Lontra canadensis*, *Enhydra lutris*, *Pteronura brasiliensis*) are excellent models for locomotor modes of Eocene whales (Thewissen and Williams 2002).

Protocetids are diverse in the morphology of their locomotor skeleton. Some of the better known forms

(*Rodhocetus*, Gingerich *et al.* 2001; *Maiacetus*, Gingerich *et al.* 2009) appear to have limbs that are longer than those of remingtonocetids, more similar to those of ambulocetids. It is possible then that pelvic paddling was also the main mode of locomotion of protocetids for which the skeleton was known. It has been suggested that protocetids had a fluke (Gingerich *et al.* 1994). In modern cetaceans, the fluke lacks a skeleton beyond the vertebrae in its axis. However, there are osteological correlates to the fluke; a vertebra near the root of the fluke has aberrant height/width proportions (Buchholtz 1998) and somewhat convex articular surfaces on its centrum (which are also present in the basilosaurid *Dorudon*, Uhen 2004). These osteological correlates suggest that known protocetids, in spite of having a powerful tail, lacked a fluke (Gingerich *et al.* 1994; Buchholtz 1998).

The fluke originated with basilosaurids. *Basilosaurus* is the largest Eocene whale, it had a long snake-like body, and probably swam with sinuous movements of its entire body. Although swimming in *Basilosaurus* has been poorly studied, the morphology of its smaller relative *Dorudon* has been well documented by Uhen (2004). This author concluded that *Dorudon* was a caudally propelled fish eater, catching prey through fast sprints.

In order to study overall shape of the locomotor skeleton, Thewissen *et al.* (1996) executed a principal component analysis of postcranial measurements. Gingerich (2003) also utilized principal components, but used a much larger comparative sample to analyze locomotor evolution in some Eocene whales. Surprisingly, Gingerich (2003) did not include any data on the tail in his analysis, even though tail-based locomotion is well-documented in semi-aquatic mammals and modern cetaceans (e.g. Fish 1996, 2000). Hence, Gingerich's (2003) results clearly identify differences in body proportions in early whales, but they may not bear on the origin of axial locomotion in cetaceans.

An important theme in the evolution of cetaceans is the loss of the hind limbs; these are large and complete in pakicetids, ambulocetids, remingtonocetids, and protocetids, but highly reduced in basilosaurids. Mysticetes and odontocetes lack external hind limbs, although all cetaceans have an internal bone in the anterior abdominal wall that represents the innominate and some have a femur and tibia. Hind limb buds are also present in dolphin embryos (figure 1). Thewissen *et al.* (2006) were able to determine that protein signaling of Hand2 and Shh leads to the reduction of hind limbs in embryos of the modern Pantropical spotted dolphin, *Stenella attenuata*.

Relatively complete innominates are preserved for raoellids, pakicetids, ambulocetids, protocetids, and basilosaurids. The pubic symphysis of *Pakicetus* and *Ambulocetus* is small, rounded, and restricted to the cranial portion of the interpubic region. A short pubic symphysis was described in the protocetids *Georgiacetus* (Hulbert 1998), and *Maiacetus* (Gingerich *et al.* 2009). In contrast

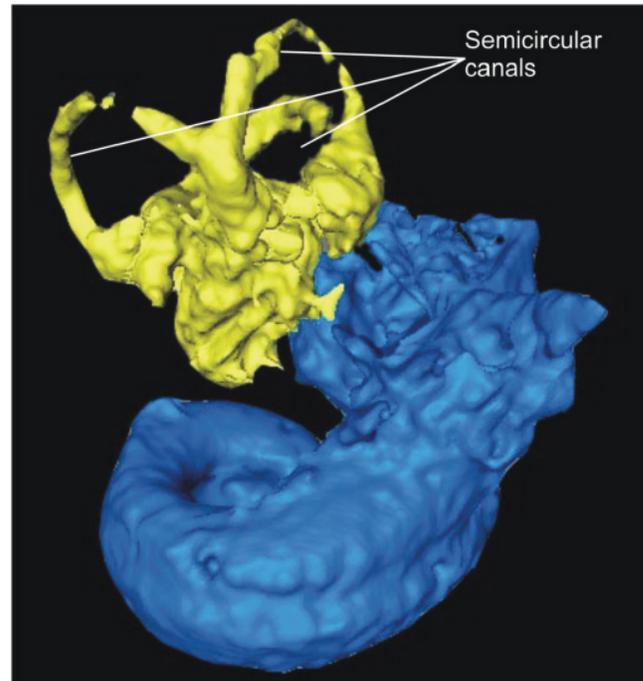


Figure 9. Reconstruction of the cavities (bony labyrinth) of the petrosal bone (inner ear) of the remingtonocetid *Andrewsiphius* (IITR-SB 2786). This image is based on CT-scans of the fossil, at intervals of 0.25 mm, that were reconstructed in a three dimensional model. The space that houses the organ of hearing is the cochlea and is blue, and part of the organ of balance, the semicircular canals are yellow. Total size of the bony labyrinth is less than 2 cm.

to these cetaceans, *Basilosaurus* had a much reduced pelvis (Lucas 1900). Gingerich *et al.* (1990) described additional elements of pelvis and hind limb of *Basilosaurus*, and provided an interpretation of its pelvis that implies that the pubic symphysis was large and unreduced in spite of the reduction of the size of the rest of the pelvis. In this interpretation (reconstructed in ventral view in figure 8A), the obturator foramen is located rostromedial to the acetabulum, and the ilium is located laterocaudal to the acetabulum. In land mammals, the ilium is cranial, and the obturator foramen mediocaudal to the acetabulum. Gingerich *et al.* (1990) probably based their inference on the irregular surface texture of one end of the innominate which is similar to that of land mammals with a large pubic symphysis. They interpreted this area as the pubic symphysis, and reconstructed left and right innominate as articulating here in a V-shaped fashion. This interpretation is not the most likely interpretation of the anatomy of *Basilosaurus*. Struthers (1893) described the pelvic girdle in *Balaena mysticetus*, a modern cetacean with relatively complete, albeit internal, hind limb elements. In *Balaena*, there are a bar-shaped innominate and femur, and a short, cartilaginous tibia (figure 8B). The posterior end of the innominate has a rugose surface similar to that in *Basilosaurus* in immature

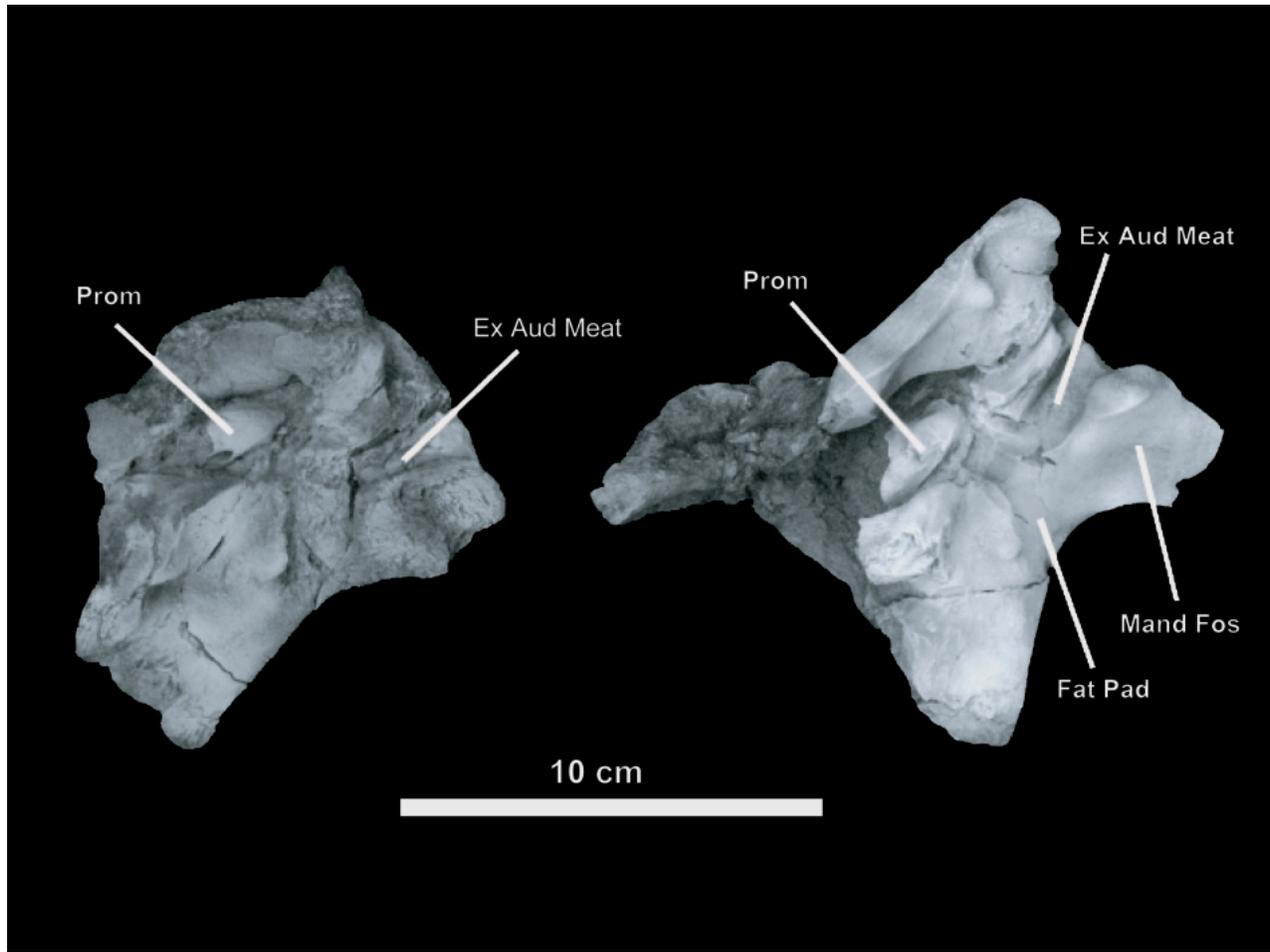


Figure 10. Ventral view of ear region of the skull of two specimens of *Remingtonocetus*, rostral down, lateral to right (IITR-SB 2529 and 2781, respectively). The tympanic has been removed to show the promontorium (Prom) under which the cochlea is located. There are two channels of sound to the ear. The first is the external auditory meatus (Ext Aud Meat), used for airborne sound. The second is the groove in which the fat pad is, and which is used for hearing underwater. Note that the two paths are separated by the mandibular fossa (Mand Fos).

individuals (Thewissen *et al.* 2009), and to the pubis of *Basilosaurus cetoides* as described by Lucas (1900). However, it is not the innominate of the opposite side that attaches here, but rather the corpus cavernosum of the penis. Interpreting *Basilosaurus* in this way is consistent with the origin of this structure in other land mammals, where the corpus cavernosum attaches to the pubis too. This alters the interpretation of the pelvic girdle as presented by Gingerich *et al.* (1990), making it more consistent with both modern land mammal anatomy and modern cetacean anatomy. Our interpretation does not change the very reasonable interpretation of the position of the hind limb of Gingerich *et al.* (1990). In *Balaena*, the hind limb is entirely internal and clearly not a good model for the much more complete hind limb of *Basilosaurus*. Our interpretation of the position of the pelvis in *Basilosaurus*, inspired as it is by modern cetacean anatomy, suggests that the most important function

of the pelvic girdle in basilosaurids relates to supporting the genitals. It is thus unlikely that left and right innominates in basilosaurids articulated in life.

5. Hearing

In mammals, the ear houses the sense organs dedicated to hearing and balance. The physics of sound in air is very different from that in water, and the cetacean ear has adapted to the watery environment (Nummela *et al.* 2007). In land mammals, the ear consists of three parts, the outer ear, middle ear, and inner ear, and its function is well understood (Geisler 1998). The outer ear is functionally an air-filled tube, the external auditory meatus. Sound, vibrations in air, pass through the external auditory meatus to the tympanic membrane, and causes this membrane to vibrate. These vibrations are carried on to a chain of three small bones

(ossicles): malleus, incus, and stapes, located in the middle ear. These ossicles form a lever system that leads to efficient sound transmission. Vibrations in the bones of the middle ear are passed on to the inner ear. Part of the inner ear is the cochlea, a fluid-filled cavity in the shape of a snail shell (figure 9). This cavity is located in a skull bone called the petrosal. Ear ossicles rarely fossilize in land mammals, but they are larger in cetaceans than in other mammals, and this increases their chances of being preserved in the fossil record. As a result, a number of ossicles have been found in Eocene whales.

In addition to this ossicular sound transmission mechanism, sound can also reach the land mammal inner ear by direct transmission through the bones and soft tissues of the skull, where different parts of the head vibrate differently, partly due to differences in inertial properties (Lombard and Hetherington 1993). This inertial mode of sound transmission occurs in all mammals, but is particularly useful in animals that live in dense substrates such as underground tunnels and water. Inertial hearing does not allow sound localization, and is usually not the main mode of sound transmission in mammals (Thewissen and Nummela 2007).

In modern odontocetes, the external auditory meatus is not present, and sounds reach the ear by passing through the mandible to a fat-filled channel to the lateral, bony wall of the middle ear, a part of the tympanic bone (Norris 1968). The lateral side of the tympanic bone has a very thin area called the tympanic window, and this is where sound is received. The tympanic window takes the place of the tympanic membrane of land mammals. From here, sound vibrations are passed on to the inner ear by a system of levers that involve the ossicles as well as a thickened lip of the tympanic bone on the medial side, the involucrum. Together these form a complicated system of levers that allow sound vibrations to pass to the inner ear (Hemilä *et al.* 1999).

These three sound transmission mechanisms – land mammal transmission, inertial transmission, and odontocete transmission – all play a role in early cetacean evolution. Because most of the elements of the hearing system are bony and fossilize, the evolution of this system is well documented by fossils (Nummela *et al.* 2004, 2007). The changes in relative importance of these mechanisms across the early cetacean clades illustrates that early whales started out with a land mammal sound transmission mechanism, and that this mechanism was modified as they took to the water. The cetacean ear went through a stage when inertial hearing was the main mode of underwater sound transmission, before the effective odontocete hearing mechanism evolved (Thewissen and Nummela 2007).

Fossils indicate that the first modifications of the middle ear leading eventually to modern odontocete sound transmission mechanisms were already present in *Indohyus*,

where the tympanic bone has an involucrum (Thewissen *et al.* 2007). As such, this structure is present in all modern and fossil cetaceans and in *Indohyus*, but not in any other mammal (Nummela *et al.* 2007; Thewissen *et al.* 2007).

The oldest known cetacean ear ossicle is the incus of *Pakicetus* (Thewissen and Hussain 1993). Although this ossicle is intermediate in size and shape between that of land mammals and modern cetaceans, Nummela *et al.* (2007) inferred that pakicetid cetaceans mainly utilized the land mammal mode of sound transmission and that their involucrum did not function as it does in modern odontocetes. It is thus likely that the involucrum of *Indohyus* is also not involved in sound transmission, and that the land mammal sound transmission mechanism, with tympanic membrane and ear ossicles, is the main mechanism. Only in later whales, such as remingtonocetids, the involucrum forms an inertial weight that allows other parts of the tympanic to be part of the sound transmission mechanism.

Clear aquatic adaptations occur in the sound transmission mechanism of remingtonocetids and protocetids (Nummela *et al.* 2004, 2007). In these whales, sound passes through the mandible and the fat pad (as evidenced by its bony canal in the lower jaw), and there is a tympanic window in the tympanic bone. Airborne sounds were also still transmitted by the external auditory meatus, and the tympanic membrane was a sound receiving area for airborne sound (figure 10). It is likely that bone conduction played an important part in the underwater hearing abilities of remingtonocetids and protocetids. This mechanism, although more effective than the land mammal transmission mechanism when submerged, caused remingtonocetids and protocetids to have poor directional hearing underwater.

In basilosaurids, the external auditory meatus is still present, and it is therefore likely that the land mammal sound transmission mechanism still was present. Inertial hearing was greatly limited by the isolation of the earbones (tympanic and petrosal) from the skull, limiting transmission of vibrations from head to ear (Nummela *et al.* 2007). This morphological isolation causes acoustic insulation, and improves the ability of the odontocete hearing mechanism to provide directional information to the ear (Nummela *et al.* 2007). In modern cetaceans, there is variation in the degree of connection between tympano-petrosal and skull, and in the most derived clades (delphinoids), there are no bony connections between ear and the rest of the skull, and the space between them is invaded by air sinuses that form an effective barrier for inertial sound.

6. Concluding remarks

The transition of whales from land to water was one of the least known transitions in the fossil record until two decades

ago. Extensive fossil collecting efforts in the past 20 years, especially in the Indian subcontinent, have turned this around. At present, the Eocene origin and evolution of whales is one of the best documented examples of macroevolutionary change. This amazing fossil record, coupled with our good understanding of form and function in modern mammals and particularly whales, allows biologists to understand organ system evolution in great detail and use the documented pattern of evolution to identify the evolutionary processes that underlie it.

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